

Morphology and Mode of Burrowing in *Siliqua patula* and *Solen rosaceus* (Mollusca: Bivalvia)

BY

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(6 Text figures)

The mode of burrowing in the Bivalvia is intimately associated with body and shell form and is also closely connected with aspects of the animal's mode of life. The morphology of many bivalves has been described, and papers by DREW (1899, 1907), JORDAN (1915), WEYMOUTH (1920), FRAENKEL (1927), STOLL (1938), QUAYLE (1949), ALLEN (1958), HOLM (1961), and ANSELL (1962) have stressed burrowing activity in the class. There is, however, little mentioned in the literature concerning the interrelationship of burrowing and morphology. This paper attempts to relate and compare these two aspects in *Solen rosaceus* CARPENTER, 1865 and *Siliqua patula* (DIXON, 1788).

Mode of Life

Solen rosaceus CARPENTER, 1865

This organism lives in a permanent burrow in which it can freely move up and down. It is found in mud flats in sheltered bays and ranges from Santa Barbara, California to Baja California, México. Its occurrence in these areas has been described by WEYMOUTH (1920) and RICKETTS (1952).

The burrowing behavior of certain species of *Solen* has been described by FRAENKEL (1927). The behavior of *Solen rosaceus* conforms to the general pattern outlined by him and is described below.

When the animal is unearthed and placed on the substratum, it first extends the foot out of the shell in an anterior direction (fig. 1a). The muscles at the tip of the foot contract causing the very tip to extend and become pointed. The foot is pushed into the soil by simultaneously extending the tip and forcing the bulk of the foot out from between the valves. This action continues until the foot is well below the soil, where it swells at the end and forms a bulbous anchor (fig. 1b). Next, the pedal retractor muscles contract, and the shell

portion of the animal is drawn into the sand toward the anchor (fig. 1c). The sequence of movements is repeated until the animal reaches the required depth in the substratum.

Movement within the burrow was not seen in *Solen rosaceus*, but it is probably the same as I have observed for *Solen sicarius* GOULD, 1846. This movement differs slightly from the movements made when the organism is re-burying itself. First, the valves open widely and grip the sides of the burrow wall (fig. 2a). Then the foot is extended to a length that is approximately equal to the shell length. Next, the tip of the foot swells and grips the burrow wall, the valves close, and the pedal retractors contract, causing the shell to move toward the anchored foot (fig. 2b).

Siliqua patula (DIXON, 1788)

This clam occurs on exposed sandy beaches, often in the zone of heavy surf, as described by WEYMOUTH (1920), QUAYLE (1941), and YONGE (1952). It ranges from the Aleutian Islands to Pismo Beach, California (BURCH, 1944). The animal lives vertically in the sand and forms no permanent burrow as do its related bay-living forms *Solen rosaceus* and *S. sicarius*. The valves are thin, but a highly developed burrowing ability keeps it from being easily unearthed and damaged by wave action. A small specimen (about 3 cm long) can rebury itself in 7 seconds, while a larger individual (about 8 cm long) takes 27 seconds. This is relatively faster than a 7 cm long *S. sicarius* which takes from 45 seconds to 11 minutes for the same operation.

Although YONGE (1952) stated that the foot of *Siliqua* functions in the same manner as that described by FRAENKEL (1927) for other genera of the Solenidae, several differences have been noted. (Compare with the description of burrowing for *Solen rosaceus*.) When burrowing, *Siliqua* first extends its foot antero-ventrally (fig.

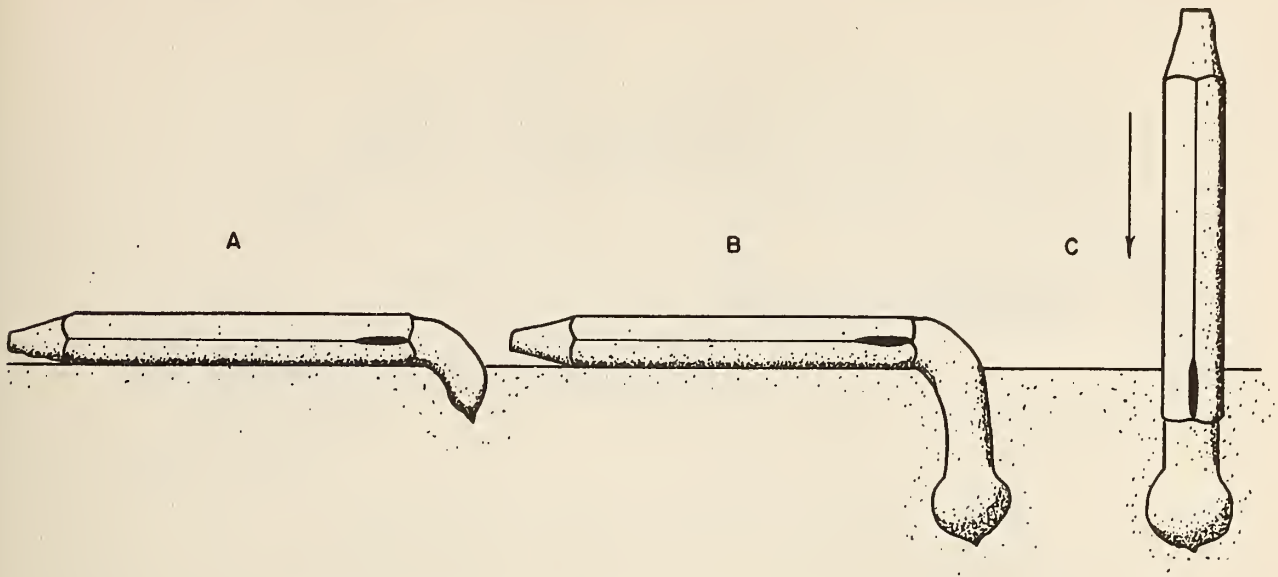


Figure 1: *Solen rosaceus*. Burrowing movements. Description in text.

3a). The foot is then thrust rapidly in an anterior direction (arrow in fig. 3a) where it is driven, pointed end first, into the sand. This one rapid motion places the foot anterior to the valves and well into the soil. The fringed margin of the foot then expands and opens out to form

an anchor in much the same way as YONGE (1959) described for *Pharus legumen* (LINNAEUS, 1758). The pedal retractor muscles then contract and pull the shell toward the anchored foot (fig. 3b). A few repetitions of this sequence are enough to bury the organism.

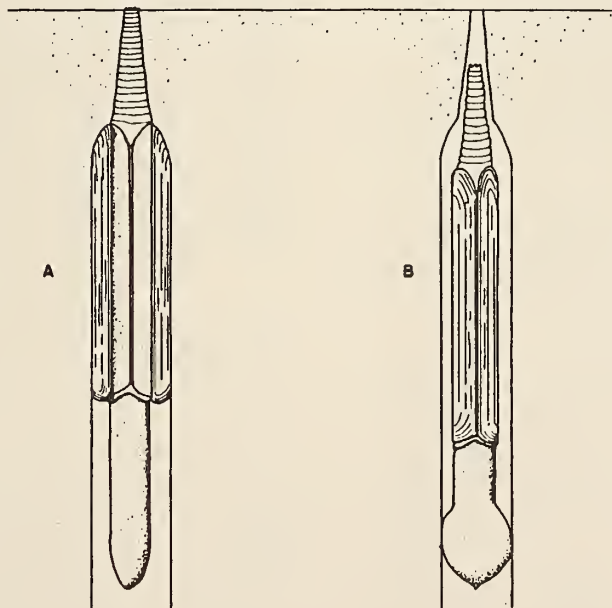


Figure 2: *Solen rosaceus*. Movement within the burrow. Description in text.

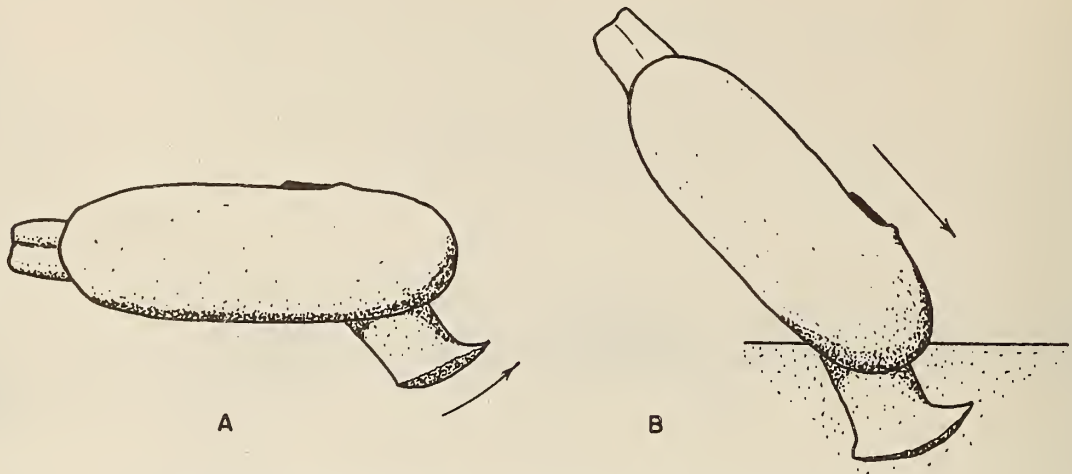


Figure 3: *Siliqua patula*. Burrowing movements. Description in text.

Morphology

Solen rosaceus CARPENTER, 1865

This animal attains a maximum length of about 6 cm (WEYMOUTH, 1920). The shell is elongated, being approximately 5 times as long as wide.

A dissection is shown in figure 4, the right valve and mantle lobe having been removed. The siphons are fused for their entire length and are about $\frac{3}{4}$ as long as the length of the shell. The inhalant siphon is protected by a ring of tentacles, while the exhalant siphon is partially enclosed by a circular flap. The siphons are annulated for their entire length, and each annulation has a fully developed set of siphonal tentacles. When the siphons are autotomized, which readily occurs when they are irritated or when the water becomes stale, a new set of tentacles is already formed and apparently ready to function.

The mantle overlying the labial palps and portions of the demibranchs is very thin, but in all other places it is muscular and thick. The edges of the mantle lobes are fused along the entire ventral margin. This restricts the pedal opening to the anterior end.

The foot is long and cylindrical, resembling a finger. It is highly mobile and can be extended to a length approximately equal to that of the shell.

The adductor muscles are inserted along the dorsal portion of the shell. The anterior adductor is large and elongated antero-posteriorly. This is not merely a posterior extension of the muscle, but as shown by OWEN (1959), the primitive dorso-ventral axis is now oriented antero-posteriorly. The posterior adductor is smaller than the anterior and its long axis runs obliquely to the long axis of the shell.

There are three attachments of the pedal muscles on each valve (fig. 4). The large anterior protractor muscle (AP) is located near the posterior margin of the anterior adductor. The fibers of this muscle extend posteriorly around the digestive diverticula and radiate out onto the foot. The anterior retractor muscle (AR) is located posterior to the anterior protractor muscle. The strands of this muscle run postero-ventrally where, near the foot, they split into two bundles and fan out onto the foot. The division of this muscle resembles the condition described for *Pharus legumen* by YONGE (1959). A small muscle (PM) is inserted onto the shell adjacent to the region of mantle thickening. The fibers pass postero-ventrally, under the anterior protractor fibers, and radiate out onto the foot. The posterior retractor muscle (PR) is the largest of the pedal muscles, being about ten times greater in area at the site of attachment than is the anterior retractor muscle. It is inserted onto the shell adjacent to and on the antero-dorsal side of the posterior adductor muscle.

Siliqua patula (DIXON, 1788)

This species attains a maximum length of about 15 cm (WEYMOUTH, 1920). The shell is elongated, being just over 2.5 times as long as high.

A dissection is shown in figure 5, the right valve having been removed. The siphons are rather short and are fused except at the very tip. Both the inhalant and exhalant openings are ringed by tentacles. The tentacles around the exhalant opening are long and thin; those surrounding the inhalant opening are short and frilled.

The mantle is fused ventrally from the siphons to a point on the margin just posterior to the umbo. Here the muscular mantle fusion is terminated and the fourth pal-

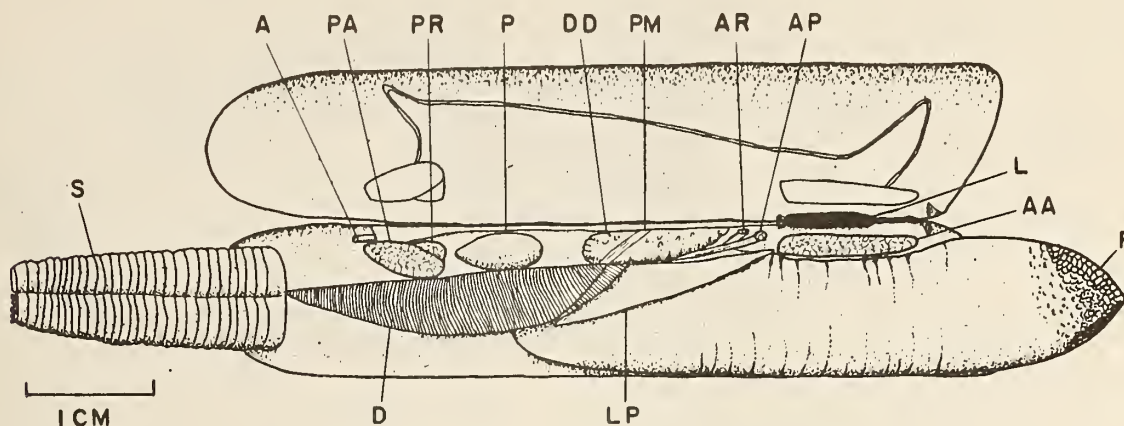


Figure 4: *Solen rosaceus*. Mantle cavity viewed from the right side.

A: anus; AA: anterior adductor; AP: anterior pedal protractor; AR: anterior pedal retractor; D: demibranchs
DD: digestive diverticula; F: foot; L: ligament; LP: labial palps; P: pericardium; PA: posterior adductor muscle;
PM: pedal muscle; PR: posterior pedal retractor; S: siphons.

lial aperture begins. The presence of this opening was first noted by OWEN (1959). He also recognized that cuticular fusion was present anterior to the fourth pallial aperture; but, because he had only preserved material with which to work, he concluded that the cuticular fusion extended to the anterior margin and that the pedal opening was there confined. The actual extent of cuticular fusion (fig. 5, CF) is very short, being about 0.8 cm in an animal 8 cm long. Thus the pedal opening is not restricted to the anterior end, but extends on the ventral edge of the shell from a point below the umbo to the anterior adductor. The entire mantle edges are fringed with tentacles, which are smaller on the postero-dorsal margin and at the site of the pedal openings.

The foot is large and oval in cross-section. Its end is pointed, and a frilled muscular fold extends from the tip to the heel.

The adductor muscles are placed near the dorsal margin. The anterior adductor is larger than the posterior, and, in both, the long axis is oriented obliquely to the long axis of the valves.

There are five insertions of the pedal muscles on each valve (fig. 5). The anterior protractor muscle (AP_1) is attached adjacent to the anterior adductor on its dorsal margin. This muscle runs postero-ventrally where it meets the muscles emanating from a second anterior attachment of the protractor muscle (AP_2). The muscles from the two insertions coalesce and continue around the digestive diverticula to the site of posterior attachment of this muscle (PP). This is in contrast to the

findings of OWEN (1959) where he stated that there is no trace of the posterior protractor muscle in this genus. The fibers emanating from the posterior protractor muscle run ventrally onto the foot and also to the anterior margins of the pericardium. The anterior retractor muscle is attached high on the shell just beneath and slightly posterior to the umbo (AR). The strands of this muscle pass ventrally to the foot. The posterior retractor muscle is large and is located adjacent to the posterior adductor on its anterior side (PR). This muscle arrangement is different than that depicted by YONGE (1952) in his study of this species, for he illustrated only two pedal insertions on each valve. He located the anterior retractor insertion posterior to the anterior adductor muscle and stated that the muscle is inserted on a rib which extends antero-ventrally from the umbo. He concluded that this rib is functionally associated with the anterior retractor muscle and serves as a strengthening ridge. This rib probably does serve to strengthen the shell, but it is not associated with the anterior retractor muscle, as this muscle is attached under the umbo.

Figure 6 shows the change in form that occurs during the ontogeny of *Siliqua patula*. Until the animal is 2.5 cm long (fig. 6a) the outline of the shell is rather oval. After attaining this size, the elongated form, characteristic of the large *Siliqua*, is assumed. YONGE (1952, 1962) stated that a byssus is present in the young post-larval stages, and this probably corresponds to the oval stage shown in figure 6a. When the byssus is lost, the animal assumes its elongated form (fig. 6b) which seems to be highly adapt-

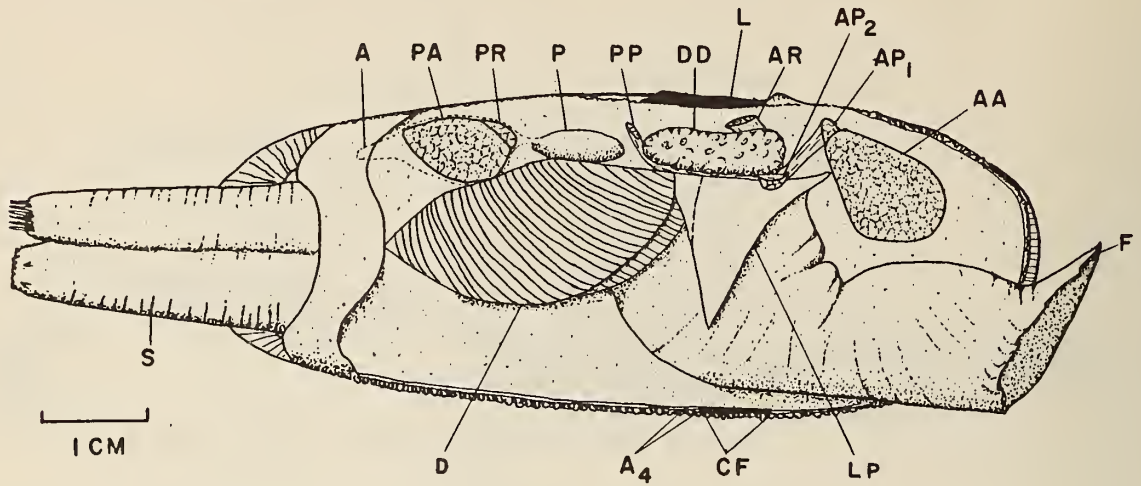


Figure 5: *Siliqua patula*. Organs seen from the right side after removal of the right valve. A₄: fourth pallial aperture; AP₁: anterior pedal protractor; AP₂: second attachment of the anterior pedal protractor; CF: cuticular fusion; PP: posterior pedal protractor. Other symbols as in Figure 4.

ed for the rapid vertical type of burrowing characteristic of the species. A phenomenon somewhat similar to this appears to occur in *Venerupis pullastra* (MONTAGU) as outlined by QUAYLE (1952), who suggested that the rapid adoption of an oval form in the early post-larval stage is advantageous for burrowing in this species.

Interrelation of Form and Burrowing

The morphology and mode of burrowing of *Siliqua patula* and *Solen rosaceus* show many differences. Both are elongated antero-posteriorly, but this condition is more pronounced in *Solen rosaceus*, the length-height ratio being approximately 2½ : 1 in large specimens of *Siliqua patula* and 5 : 1 in *Solen rosaceus*. The elongated form is an adaptation for vertical burrowing (YONGE, 1952).

In *Solen rosaceus*, foot movements are confined to an antero-posterior direction. Hence the long axis of the shell

is parallel to the burrowing direction, which decreases resistance to the substratum. Corresponding to the movement of the foot is the growth of the anterior adductor, which extends mainly along the antero-posterior axis of the body. This muscle is located adjacent to the ligament, and, because it is in such close proximity to the ligament, a large muscle would probably be more efficient in counteracting the opening moment of the ligament. The only direction in which this muscle can grow without hampering the movements of the foot is in the antero-posterior plane.

This muscle is elongated in many species of the genus *Solen*, and it reaches its maximum extent in the genus *Ensis*. There is a correlation between the posterior extension of this muscle and the reduction in relative size of the posterior adductor muscle. In *Solen rosaceus* and *S. sicarius*, the anterior adductor is elongated so that its posterior end lies opposite the posterior end of the liga-

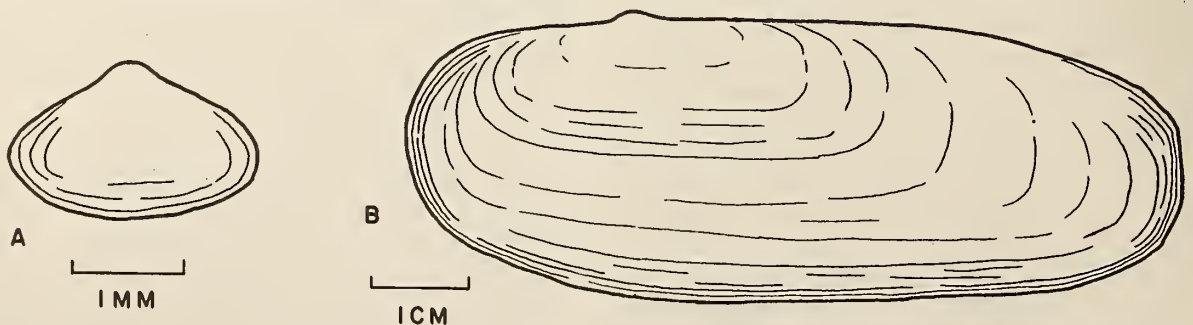


Figure 6: *Siliqua patula*. Change in form during ontogeny. Figure 6 A - a specimen 2.5 mm long; Figure 6 B - a specimen 80 mm long. Anterior end to the left.

ment (fig. 4). In these forms, the anterior adductor is about 1.5 times as large as the posterior. In species of *Ensis*, there is considerable growth of the anterior adductor posterior to the ligament and the posterior adductor is correspondingly quite small, the anterior adductor being at least three times as large as the posterior. As the growth of the anterior adductor moves posterior to the ligament, which occurs in those forms with an extreme reduction of depth, the closing moment of this muscle will tend to close the shell along its entire length; and the function of the posterior adductor is taken over, to a degree, by the anterior. OWEN (1959) stated that the reduction of the relative size of the posterior adductor is due to the extension pallial attachment in the posterior embayment of the mantle. This also appears to be a contributing factor. There are several changes in morphology that accompany the increasing loss of depth in these organisms. These include the greater growth of the anterior adductor posterior to the ligament, the reduction in size of the posterior adductor, and the occurrence of pallial attachment posterior to the posterior adductor.

In *Siliqua patula*, the foot movements differ from *Solen rosaceus*. In *Siliqua*, the foot is extended antero-ventrally, not directly anteriorly. The foot is then thrust anteriorly as shown by the arrow in figure 3a. Corresponding to the pedal movements is the placement of the anterior adductor. The direction of growth of this muscle is not confined to the antero-posterior plane, but the main growth axis is in an antero-ventral direction.

The posterior retractor muscle is larger than the anterior in both species. The size and placement of the posterior retractor is closely associated with the functioning of the foot during burrowing. When the foot is anchored, there is approximately a straight line between the anchor and the site of attachment of this muscle. When the muscle contracts, it exerts its pull nearly parallel to the long axis of the shell. This tends to keep the movements of the foot parallel to the long axis of the valve and insures that the long axis of the shell is not exposed to the resistance of the substratum.

In both species, the ventral mantle is fused. In *Solen rosaceus*, the fusion extends from the ventral edge of the inhalant siphon to a point on the ventral margin immediately under the umbo; that is, the mantle is fused along the entire ventral margin. The fused mantle aids in keeping foreign particles out of the mantle cavity and also, coupled with the rigid housing provided by the teeth and ligament articulation, confines the foot movements to the antero-posterior axis. In *Siliqua patula*, the fusion of the ventral mantle is not so extensive. Muscular cross fusion extends from the siphons to a point on the

ventral margin just posterior to the umbo (fig. 5), i. e. about two thirds of the ventral margin are fused. Tissue fusion is terminated at the fourth pallial aperture, but there is limited cuticular fusion anterior to this. The pedal gape is not confined to the anterior end as mentioned by OWEN (1959), but foot movements do occur in the antero-ventral direction as mentioned by YONCE (1952).

The shape of the foot in the two species is quite dissimilar. In *Solen rosaceus* it is finger-like, whereas in *Siliqua patula* it is cylindrical, but pointed on its dorsal and flattened on its anterior extremities (compare figs. 4 and 5). In *Siliqua patula*, a frilled muscular flap extends from the tip to the heel of the foot. This flap opens out and inflates to form an anchor, whereas in *Solen rosaceus* the end of the foot merely swells to form an anchor, there being no muscular flap present. The foot of *Solen rosaceus* is well suited for movement within a permanent burrow (fig. 2). *Siliqua patula*, which lives in the surf zone, constructs no such burrow, and its pointed foot is well adapted to the rapid type of digging characteristic of this animal. *Solen rosaceus* requires many probes of the foot to bury it sufficiently to form an anchor, whereas in *Siliqua patula* one quick thrust of the foot usually places it well into the substratum. This is an important factor contributing to *Siliqua patula*'s rapid burrowing and is a useful adaptation for maintaining positional stability in its surf habitat.

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Lumpers and Splitters

BY

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Part I: The Generic Division of Cowries

LINNAEUS (1758) has established the genus *Cypraea* for 42 so-called species, arranged in several groups according to superficial characters of the shells. The first monographer of the cowries, J. E. GRAY (1824 to 1828), has described 116 living and fossil species as members of this one genus also. The subsequent well known iconographies on living cowries, edited chiefly for use of collectors by SOWERBY (1832 to 1837), KIENER (1843 to 1845), REEVE (1845 to 1846), SOWERBY (1870), WEINKAUFF (1881), and ROBERTS (1885) also united all cowries denticulate on both lips of the shell to the genus *Cypraea*, including two species of Sulcocypraeinae (*Cypraea adamsonii* SOWERBY and *C. pustulata* LAMARCK, which anatomically approach the Amphiperatidae more than the Cypraeidae) and many species of Triviidae, which family has been removed from the Cypraeacea (= Cypraeidae and Am-

phiperatidae, both with a triangular osphradium) to the Lamellariacea (see Zoological Record 92 for 1953, p. 82). In the same way, HIDALGO (1906 to 1907) enumerated in his monograph 222 living species of "*Cypraea*" (Triviidae etc. included) in alphabetical order so that comparison of allied species becomes difficult. Even I myself lumped all cowries (Triviidae excluded) when beginning my special studies (SCHILDER 1922, 1924a).

Sixty years before, however, TROSCHEL (1863) examining the radula, divided the family "Cypraeacea" into 8 genera and subgenera, well separating them from the family "Triviacea" (genera *Erato* and *Trivia*); the Amphiperatidae had been split into several genera a long time before. Another step in splitting up the cowries has been made by JOUSSEAUME (1884) considering both living and fossil species: this "auteur mal inspiré" (CROSSE) has distinguished 36 coordinate genera, many of which